

INFLUENCE OF AGE AND PREY AVAILABILITY ON BALD EAGLE FORAGING BEHAVIOR AT GLACIER NATIONAL PARK, MONTANA

ROBERT E. BENNETTS^{1,2} AND B. RILEY MCCLELLAND^{3,4}

ABSTRACT.—It has been hypothesized that foraging tactics and ability of Bald Eagles (*Haliaeetus leucocephalus*) are influenced by age, phenotype, and prey availability. We studied the influence of eagle age class and prey availability of kokanee salmon (*Oncorhynchus nerka*) on foraging behavior of Bald Eagles during autumns of 1983 and 1984 at Glacier National Park, Montana. The relative use of foraging tactics differed among four age classes of eagles during both years. Stooping was the most successful tactic and was most frequently used by older birds. The relative use of stooping increased with age and the use of ground piracy tended to decrease with age. The relative use of different foraging tactics also reflected changing prey availability. During 1983, when lower numbers of salmon precluded accumulation of carcasses, eagles rarely used ground tactics (i.e., scavenging and ground piracy). In 1984, when salmon carcasses accumulated in large numbers, all age classes used ground tactics, which became the predominant foraging method of younger eagles. Our results support the hypotheses that the ability to obtain food increases with age and that eagles forage by methods for which their age class is most suited based on morphology (e.g., size and wing loading) and experience. Received 30 Sept. 1996, accepted 1 Feb. 1997.

During the autumns of 1983 and 1984 we assessed the influences of age and prey availability on foraging methods and prey capture success of Bald Eagles in Glacier National Park (GNP), Montana. The foraging ecology of wintering Bald Eagles has been the focus of previous studies (e.g., Stalmaster and Plettner 1992, Brown 1993); however, the concentration of Bald Eagles at GNP offered several unique characteristics. Bald Eagle concentrations based on prey other than salmon (e.g., Stalmaster and Plettner 1992, Brown 1993) usually consist of multiple prey types and habitats which can confound assessments of the influence of prey availability. In contrast, the food resource for Bald Eagles at GNP was almost exclusively a single species, kokanee salmon (*Oncorhynchus nerka*), of one age class (spawners mostly four years old). Fish varied greatly in abundance and vulnerability to capture among and within seasons (McClelland et al. 1982, Bennetts and McClelland 1991). Consequently, we were able to assess the influence of prey availability on the foraging

¹ Division of Biological Sciences, Univ. of Montana, Missoula, Montana 59812.

² Present Address: Florida Cooperative Fish and Wildlife Research Unit, P.O. Box 110450, Univ. of Florida, Gainesville, Florida 32611-0450.

³ School of Forestry, Univ. of Montana, Missoula, Montana 59812.

⁴ Present Address: P.O. Box 366, West Glacier, Montana 59936.

tactics and success of Bald Eagles in an environment that minimized confounding variation. Also, in contrast to most other eagle concentrations based on spawning salmon, the salmon at GNP were small enough to be carried in flight by eagles. At other salmon-based concentrations (e.g., Stalmaster and Gessaman 1984, Hansen 1986, Knight and Skagen 1988), the potential for eagles to use aerial attacks (e.g., stooping or aerial piracy) to capture salmon was largely precluded because of the large size of salmon. Consequently, a broader spectrum of foraging methods was possible at GNP compared to other salmon-based concentrations.

Previous studies on the effects of age on eagle foraging ecology generally have assigned birds to one of two age classes (adults and immatures). Because Bald Eagles usually require ≥ 4.5 years to acquire definitive plumage (McCullough 1989), grouping all immatures together combines several different age classes. Thus, the development of foraging ability from juvenile through several subadult stages may be masked. We assessed the influence of relative age on foraging ecology based on four age classes and could, therefore, more effectively evaluate how foraging ability changes with age.

STUDY AREA AND METHODS

GNP (approximately 48°30'N, 114°00'W) is adjacent to the Canadian border in northwestern Montana and is bisected by the Continental Divide. Beginning in the late 1930's, Bald Eagles were attracted to non-native spawning kokanee salmon in Lower McDonald Creek (LMC) in GNP. An annual concentration of Bald Eagles persisted until 1986, when the salmon population began a precipitous collapse (Spencer et al. 1991). LMC flows 4 km from the outlet of Lake McDonald to the confluence with the Middle Fork of the Flathead River. The average width of LMC during the autumn is approximately 25 m; it is interspersed with deep pools, shallow runs with gravel beds, and riffles.

Bald Eagles at LMC were counted weekly during both years using the procedures described by McClelland et al. (1982). These counts were standardized to enable meaningful comparisons among and within years, and were designed to minimize the chance of repeatedly counting the same birds.

Age classes.—Eagles were assigned to one of four age classes based on plumage characteristics subsequently described by McCullough (1989). Our juvenile age class corresponded to the "Juvenal Plumage" described by McCullough (1989) for birds one-half year old. Early subadults corresponded to the "Basic I" and "Basic II" plumage classes for birds that were 1½ and 2½ years old, respectively. Late subadults corresponded to the "Basic III" plumage class for birds that were 3½ years old. Eagles appearing to have a completely white head and tail were classified as adults, corresponding to McCullough's (1989) "Basic IV" and "Definitive" plumage classes for birds that were 4½ and >4½ years old, respectively. We did not attempt to distinguish between Basic IV and definitive plumage classes or between Basic I and Basic II classes because of the potential for errors under field conditions.

Prey availability.—Prey availability was assessed both quantitatively and qualitatively. Salmon counts were conducted bi-weekly by Montana Department of Fish, Wildlife, and Parks (MDFWP; Fraley and McMullin 1983, Fraley 1984). Two biologists snorkeled LMC, independently estimating the number of live salmon at each pool, run, and riffle; the two

counts were averaged for a final estimate. Although not conducted consistently, MDFWP biologists also counted numbers of dead salmon when conditions allowed. Descriptive accounts of spawning behavior also were recorded during these counts. Based on studies of tagged individuals, the residence time of individual salmon at LMC was estimated to be 6–8 weeks (Fraley 1984). During this time kokanee exhibited four major behavioral phases: (1) courtship, (2) redd construction, (3) egg deposition, and (4) redd maintenance (Fraley and McMullin 1983). Speculating that these spawning phases and the corresponding changes in physical condition of the salmon influenced their availability to eagles, we assigned each two-week time period (with the bi-weekly count as midpoint) to a spawning phase based on the predominant spawning behavior occurring during that period. We also included one additional phase representing the time period after spawning behaviors ceased. Spawning phases were characterized as: (1) *Courtship*—When kokanee first arrived they were in strong physical condition. They congregated in deep pools and generally were unavailable to eagles. This activity occurred primarily before eagles began congregating in large numbers; therefore, it was not included in our sample of foraging observations. (2) *Redd construction*—Some salmon ventured into shallower water and began constructing redds. Salmon remained in good physical condition, but spawners in shallow water became vulnerable to aerial attacks by eagles. About 10% of the salmon deposited eggs during this phase. (3) *Egg deposition*—Egg deposition peaked and most salmon were in some stage of spawning, where they were highly vulnerable to stooping attacks by eagles. Physical condition of salmon deteriorated after spawning. Dead salmon became available for scavenging, but live salmon provided more foraging opportunities. (4) *Redd maintenance*—Live salmon still outnumbered dead salmon, but almost all were in severely weakened condition. Numbers of dead salmon peaked during this phase and carcasses typically accumulated. Salmon were vulnerable to all foraging tactics. (5) *Post spawning*—Few live salmon remained. Dead and dying salmon were rapidly taken by eagles or other scavengers (e.g., grizzly bears [*Ursus arctos*]). Remaining carcasses accumulated only in deep pools, where they were unavailable to eagles.

Foraging methods.—Data were collected four days per week during the autumns of 1983 and 1984 from two viewing areas (previously described by Bennetts and McClelland [1991]) along LMC. Three two-hour observation periods were conducted each day; periods alternated between viewing areas. The morning observation period began 30 min after sunrise. The evening period ended 30 min before sunset; a mid-day period was mid-way between the morning and evening periods.

Foraging attempts were characterized as (1) stooping, (2) scavenging, (3) aerial piracy, or (4) ground piracy. We defined stooping as an eagle coming to within 1 m of the water surface during a dive that was initiated from either a perch or the air. Stooping was directed at live or floating dead salmon. When scavenging, an eagle walked or waded to an unattended dead salmon. In aerial piracy, a pursuing eagle came within 1 m of a flying eagle carrying a salmon (Bennetts et al. 1990). Ground piracy occurred when an eagle attempted to steal from another eagle on the ground. Initiation of this foraging method was from the ground, air, or a perch. We distinguished between aerial and ground piracy because these foraging tactics required different skills. For each attempt, we recorded the age class of the foraging eagle, foraging method, and whether the bird was successful.

Foraging success.—We used two measures of foraging success. First, we measured foraging success on a per-attempt basis. We considered an attempt successful if the foraging bird maintained possession of the prey item for at least 15 s. Scavenging could not be included in this analyses; by definition, the act of walking or wading to an unattended prey item resulted in a successful attempt. Because we could not discern the motive of a bird walking or wading in the absence of a prey item, we did not attempt to classify such behavior

as a scavenging attempt. If the prey item was obtained by displacing another bird, it was piracy rather than a scavenging attempt. We did not observe more than one eagle feeding on the same fish. Fish take was estimated as the number of fish taken by a given age class per hour divided by the average number of eagles of that age class counted. A minimum of two ($\bar{x} = 2.9/\text{observation period}$) censuses of the number of birds of each age class present in our viewing area were taken during each observation period.

Analyses.—Using log-linear models, we explored the effects of age, year, and spawning phase on the use of different foraging tactics. Because a fully saturated model (i.e., with all possible main effects and interactions) had 128 parameters, many of which were not identifiable or estimable, we began this analysis by first exploring the effect of individual first- and second-order interactions (i.e., two and three-way interactions). This is analogous to the preliminary univariate tests suggested by Hosmer and Lemeshow (1989) for logistic regression. To test these interactions we used a likelihood ratio test of saturated models (only for effects being evaluated) and the same model without the interaction being tested. Similarly, we tested main effects using a likelihood-ratio test between a full main-effects model and models lacking each main effect individually. We then used a combination of likelihood ratio tests and Akaike's Information Criteria (AIC) (Akaike 1973, Shibata 1989) to determine the most parsimonious model based on all combinations of effects indicated from our preliminary exploration. In contrast to likelihood ratio tests, which are used for pairwise comparisons of nested models, AIC is used more as an optimization tool for any number of models, nested or not. Models with AIC differences <2 were not considered as statistically significant (Sakamoto et al. 1986).

We tested the influence of age, year, spawning phase, and foraging tactic on success (per attempt) using logistic regression with success as a binary response variable. We began with a univariate analyses of each main effect. Because the potential contribution of main effects to interactions may be masked at this step, we initially used a liberal rejection criteria of $\alpha = 0.25$ (Hosmer and Lemeshow 1989). We then constructed a model including all main effects meeting the above criteria. At this and all subsequent steps of the analysis, we used a rejection criteria of $\alpha = 0.05$. We then used a combination of likelihood ratio tests and AIC to test for the inclusion or rejection of interaction terms (Hosmer and Lemeshow 1989).

We tested for the effects of age, foraging tactic, spawning phase, and year on fish take per hour using an offset log-linear model (Agresti 1990). An offset model is an extension of a log-linear model in that the number of fish for a given cell is modeled as a function of their exposure (risk) to eagles such that: $\log(f_{ij}/E_{ij}) = \beta_0 + \beta_1 \dots \beta_k$, where f_{ij} is the number of fish captured for a given cell, E_{ij} is the exposure (total eagle hours from censuses), β_0 is the intercept, $\beta_1 \dots \beta_k$ are the main effects (i.e., age, year, tactic, and spawning phase) plus any interaction effects.

RESULTS

Prey availability.—Salmon began arriving at LMC in September of both years; however, eagles did not begin to congregate in large numbers until October and November (Fig. 1). The peak salmon count was substantially lower in 1983 (34,200) than in 1984 (86,500) and occurred approximately two weeks earlier in 1983. During both autumns, the peak abundance of live salmon occurred during the redd construction phase. During 1983, the highest number of dead salmon (2870) was counted during the redd maintenance phase, when peak accumulations probably occurred. The lower number of salmon and rapid consumption by pred-

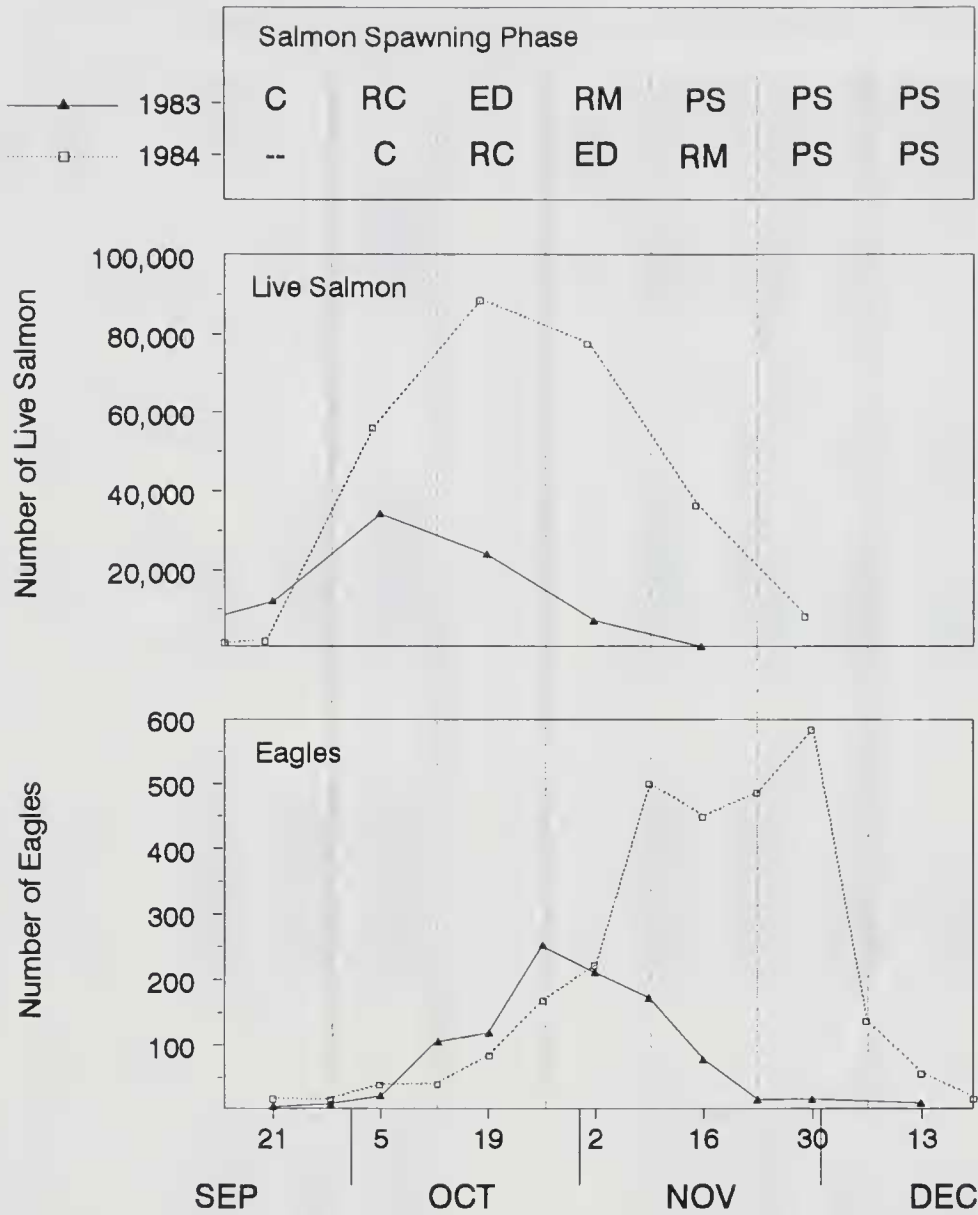


FIG. 1. Spawning phase, number of live salmon, and number of eagles counted during each two-week time period of this study. Salmon spawning phases were courtship (C), redd construction (RC), egg deposition (ED), redd maintenance (RM), and post spawning (PS).

ators and scavengers largely precluded accumulations of salmon carcasses in 1983. During 1984, the peak count of dead salmon (4500) occurred during the egg deposition phase, approximately two weeks prior to peak accumulations. High numbers of live salmon and decomposition of carcasses precluded counting dead salmon during the latter part of 1984. Thus, peak numbers of dead salmon in 1984 were unknown, but were >4500 and substantial accumulations of carcasses were readily apparent.

Foraging methods.—We observed 1485 foraging attempts by Bald Ea-

TABLE 1

TERMS AND THEIR CORRESPONDING CONTRIBUTION TO OUR FINAL (MOST PARSIMONIOUS) LOG-LINEAR MODEL OF THE INTERACTIONS BETWEEN FORAGING TACTICS AND AGE, YEAR, AND SPAWNING PHASE BY BALD EAGLES

Source	χ^2	df	Prob > χ^2
Age ^a	271.25	3	<0.001
Tactic ^a	92.75	3	<0.001
Year ^a	37.12	1	<0.001
Phase ^a	30.94	3	<0.001
Tactic*Age	187.50	9	<0.001
Tactic*Year ^b	7.55	3	0.056
Tactic*Phase	62.76	9	<0.001
Tactic*Year*Phase ^c	63.74	4	<0.001

^a Log-linear models are intended to detect interactions; however, main effect terms were retained to account for marginal totals.

^b Model selection procedures indicated similar fit of models with and without this term. We retained this term to better account for its contribution to the three-way interaction.

^c We did not have any observations during the redd construction phase of 1983; thus, some cells had structural zeros.

gles at LMC (301 during 1983 and 1184 during 1984). Our final log-linear model indicated that the foraging tactics used by Bald Eagles differed substantially among age classes, between years, and among spawning phases within years (Table 1) and several patterns emerged from this analysis (Fig. 2). Relative use of stooping increased with age class during both years. Younger birds correspondingly scavenged and used ground piracy more than older birds, particularly in 1984. Juveniles and early subadults also used aerial piracy more than older birds did in 1983.

One of the most pronounced differences between years was the relatively high use of ground tactics (i.e., scavenging and ground piracy) during 1984. The use of these tactics was almost completely lacking by adults and late subadults during 1983, when these tactics were used by juveniles and early subadults only during the egg deposition phase.

The relative use of stooping by younger birds tended to increase over time (i.e., among successive spawning phases) in 1983; however, use of this tactic tended to decrease over time for all age classes during 1984. The use of ground piracy by juveniles was completely lacking during the redd construction phase of 1984, but became the most frequently used tactic for this age class during later time periods.

Foraging success per attempt.—Our final logistic regression model indicated that foraging success per attempt was influenced by tactic, year, and spawning phase (Table 2). Based on a likelihood-ratio test, age had only a marginal effect on success per attempt ($\chi^2 = 5.30$, 3 df, $P = 0.15$) and AIC for models with and without an age effect also were similar

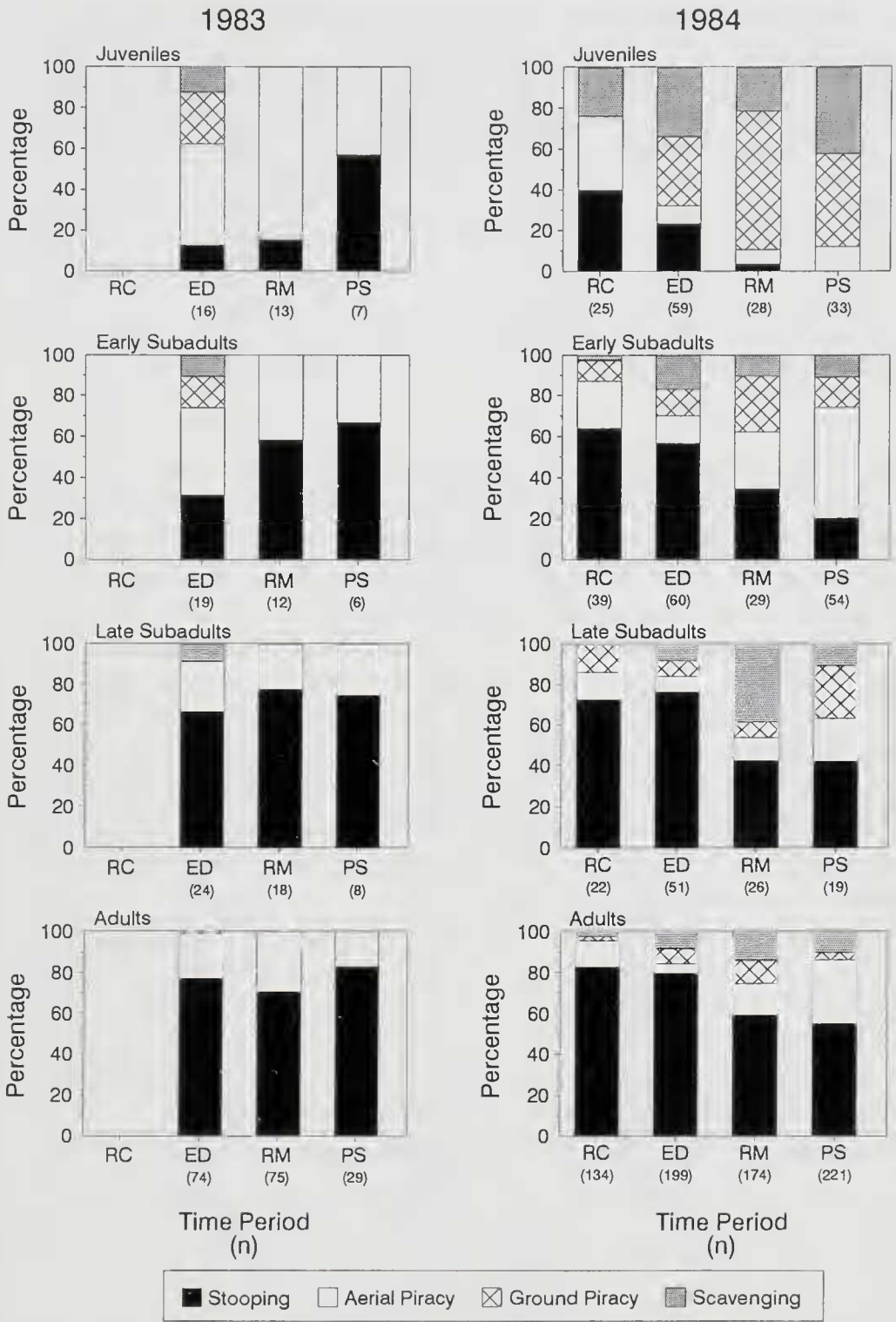


FIG. 2. Percentage use of foraging tactics by age class during spawning phases, 1983 and 1984. Salmon spawning phases were: redd construction (RC), egg deposition (ED), redd maintenance (RM), and post spawning (PS).

TABLE 2

TERMS AND THEIR CORRESPONDING CONTRIBUTION TO OUR FINAL (MOST PARSIMONIOUS) LOGISTIC REGRESSION MODEL OF THE INFLUENCE OF FORAGING TACTIC, YEAR, AND SPAWNING PHASE ON SUCCESS (PER ATTEMPT) OF FORAGING BALD EAGLES

Source ^a	χ^2	df	Prob > χ^2
Year	6.70	1	0.009
Tactic	159.91	2	<0.001
Phase	8.65	3	0.034

^a Scavenging was not included in this analysis because all attempts, by definition, were successful.

(AIC = 1586.90 and 1586.20 for models with and without an age effect, respectively). Although AIC indicated that models with and without an age effect both were adequate, we did not retain an age term in our final model based on the principal of parsimony. No interaction terms were supported by our data based on either likelihood-ratio tests or AIC.

Foraging tactic had the most pronounced influence on success per attempt (Table 2). Success was highest for stooping and lowest for aerial piracy (Fig. 3). Success of stooping was generally higher in 1984 than in 1983. Variation among spawning phases occurred; however, with the exception of aerial piracy during 1983, there was no apparent systematic pattern to this variation. Except during 1983 when success of aerial piracy increased 24% over time, use of foraging tactics among spawning phases varied up to 16% in no apparent pattern.

Our analysis did not indicate a difference among age classes in foraging success per attempt. Juveniles did, however, have the lowest (albeit insignificant) success per attempt at stooping (53%) compared to early subadults (60%), late subadults (57%), and adults (68%). In addition, stooping attempts by juveniles generally were on floating dead fish in calm water. These attempts posed relatively little difficulty in comparison to submerged live fish often taken by adults.

Foraging success per hour.—Fish take per hour was influenced by age, foraging tactic, year, spawning phase, and several interactive effects (Table 3). Overall, fish take increased with age during both years, although intake for each age class was lower in 1983 than in 1984 (Fig. 4). Fish take by stooping was substantially higher than for any other foraging tactic (Fig. 5). Fish take by scavenging and by ground piracy were the next most profitable in 1984. During 1983, fish take using each of these tactics was less than by aerial piracy. During 1983, fish take increased with age for stooping and scavenging, but decreased with age for aerial piracy (Fig. 6). During 1984, fish take increased with age for stooping

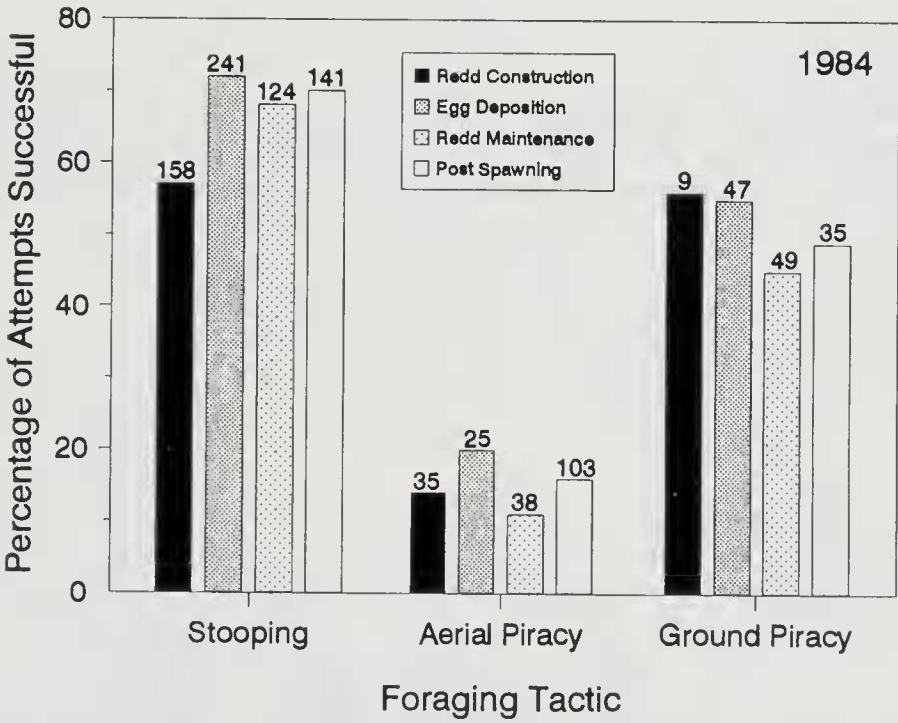
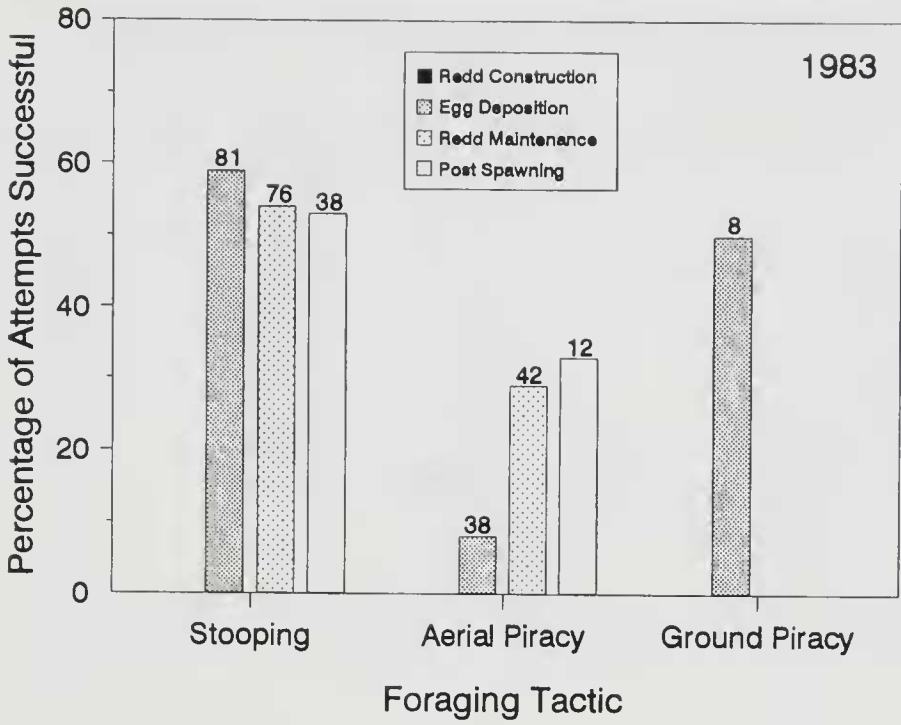


FIG. 3. Percentage of successful foraging attempts by foraging tactic and spawning phase, 1983 and 1984. Above each bar is the number of attempts on which percentage is based.

TABLE 3

TERMS AND THEIR CORRESPONDING CONTRIBUTION TO OUR FINAL (MOST PARSIMONIOUS) OFFSET LOG-LINEAR MODEL OF THE INFLUENCE OF FORAGING TACTIC, YEAR, AND SPAWNING PHASE ON FORAGING SUCCESS OF BALD EAGLES MEASURED AS FOOD INTAKE PER UNIT TIME

Source	χ^2	df	Prob > χ^2
Age ^a	230.19	10	<0.001
Year ^a	119.50	15	<0.001
Tactic ^a	716.06	24	<0.001
Phase ^a	155.34	15	<0.001
Age*Tactic	99.70	9	<0.001
Age*Year	11.04	3	0.012
Tactic*Year	54.03	3	<0.001
Tactic*Phase	44.72	3	<0.001
Phase*Year	32.51	3	<0.001

^a Because a main effects model (i.e., one model with all main effects but no interactions) did not fit the data ($P < 0.001$), significance of each main effect was determined using a likelihood ratio test between the selected model and a model lacking all terms using that main effect (including interactions). Degrees of freedom for main effects reflect this approach.

and aerial piracy, but decreased with age for scavenging and ground piracy.

During both years, fish take was highest during the egg deposition phase (Fig. 7). We did not make foraging observations during the redd construction phase during 1983 because of the scarcity of eagles during this period. Fish take decreased among each consecutive spawning phase

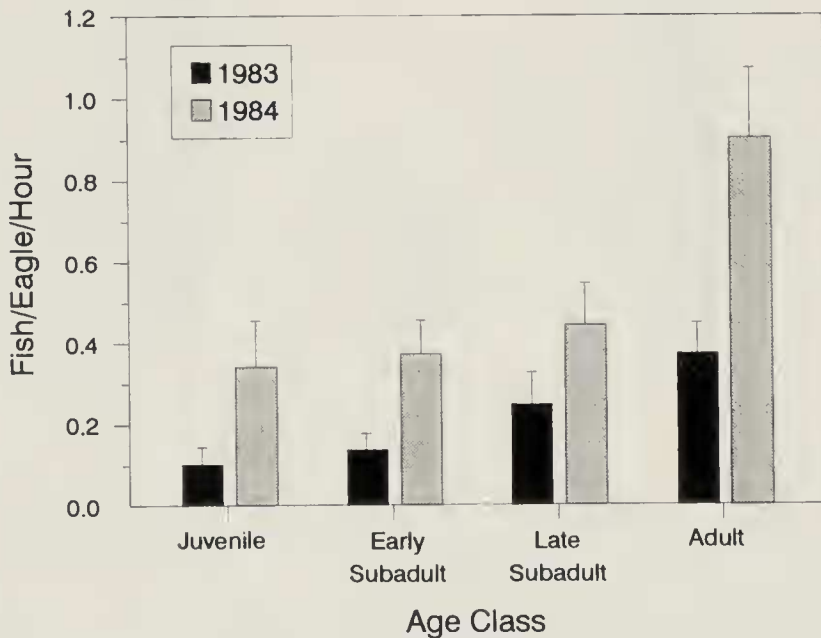


FIG. 4. Mean (+1 SE) fish take per hour by eagle age class, 1983 and 1984.

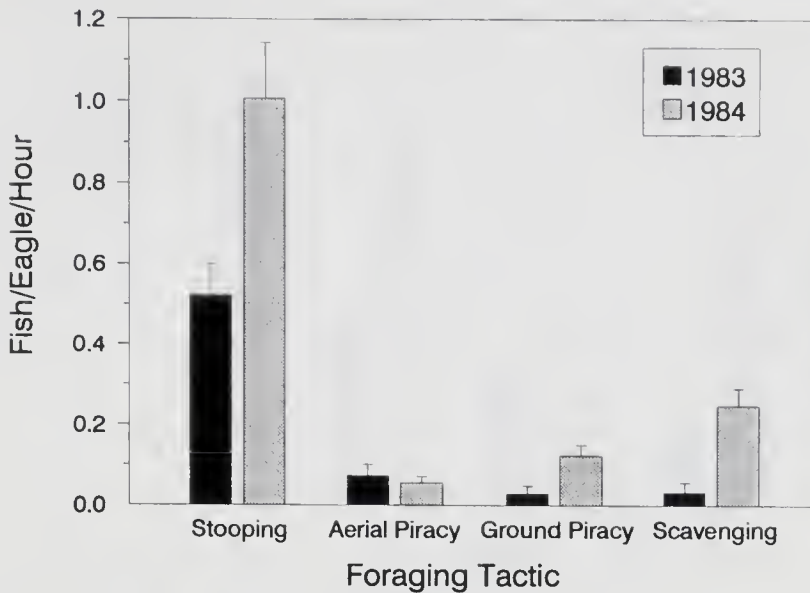


FIG. 5. Mean (+1 SE) fish take per hour by foraging tactic, 1983 and 1984.

during 1983, but showed an increase between the redd maintenance and post-spawning phases in 1984.

DISCUSSION

Influence of age on foraging behavior.—Hansen (1986) hypothesized that Bald Eagles use foraging methods for which they are phenotypically suited. Our data at LMC indicated that the ability of Bald Eagles to obtain food is dependent on their morphology (e.g., size and wing loading), experience, and possibly hunger level. Compared to younger age classes the aspect ratio, wing loading, and tail/wing ratio of adult Bald Eagles probably are better suited to the type of flight required to capture live prey (Harmata 1984). The relative use of stooping, which was the predominant and most successful method of capturing live prey at LMC, increased with age.

In addition to morphological differences among age classes, Bald Eagles may increase foraging skill through experience gained with age. Foraging methods most frequently used by younger eagles, particularly juveniles, required the least skill (i.e., ground approaches to prey rather than flying). Stooping and aerial piracy required not only detection of the prey, but also agility and precise timing, in contrast to scavenging which primarily required detection. Ground piracy probably requires more skill than does scavenging, but the host usually is stationary on the ground, often enabling even a juvenile's awkward approach to be successful. This appears to contradict Hansen's (1986) view that piracy requires more skill than hunting; however, foraging options at Hansen's study site on the

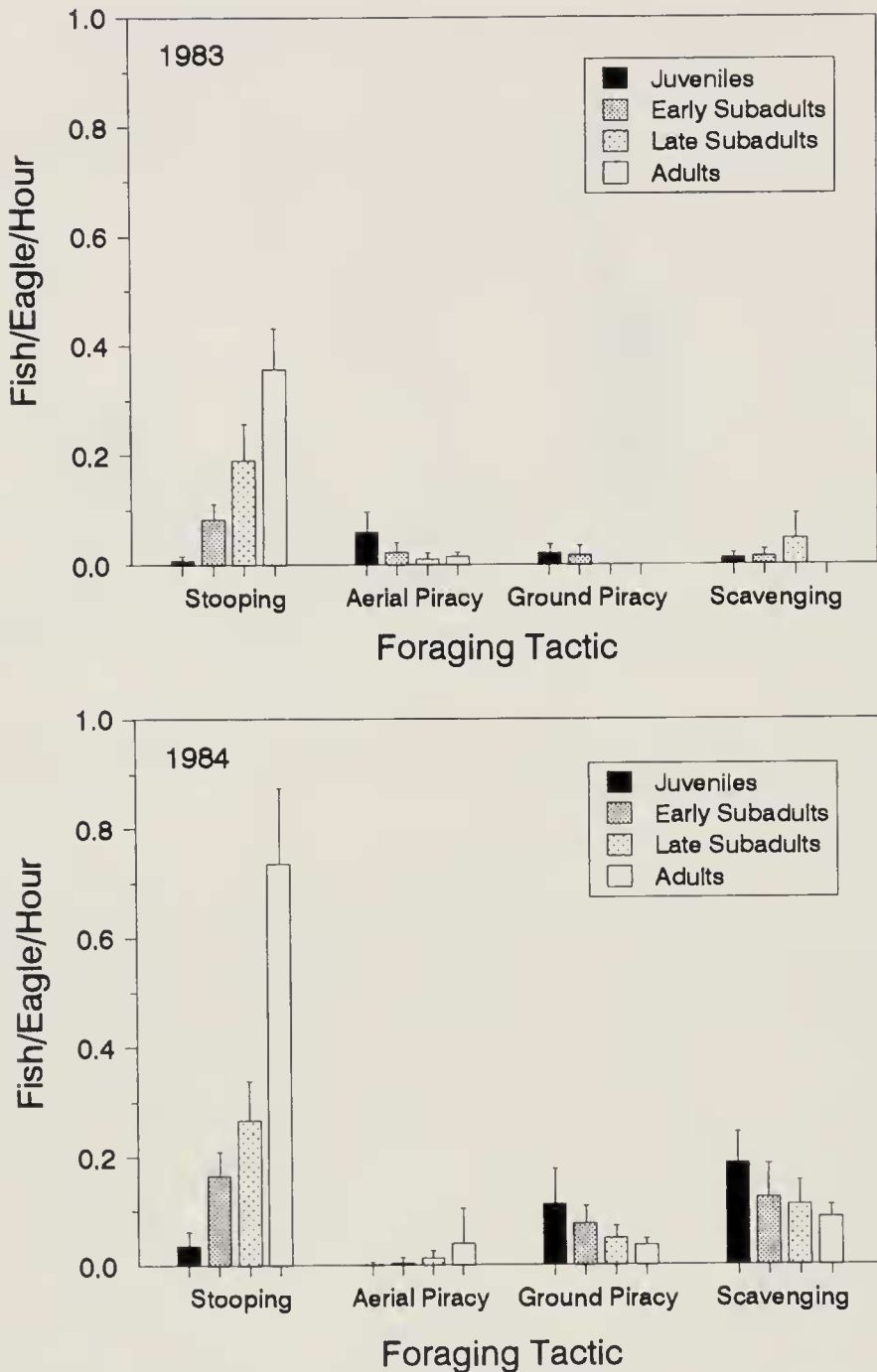


FIG. 6. The mean (+1 SE) fish take per hour by age class and foraging tactic, 1983 and 1984.

Chilkat River in Alaska differed markedly from the conditions at LMC. Salmon on the Chilkat River averaged 4.3 kg (Hansen 1986), whereas kokanee at LMC averaged 0.49 kg in 1983 and 0.33 kg in 1984 (MDFWP, unpubl. data). The larger prey on Hansen's (1986) study site precluded the use of stooping and aerial piracy or the taking of live prey. Thus,

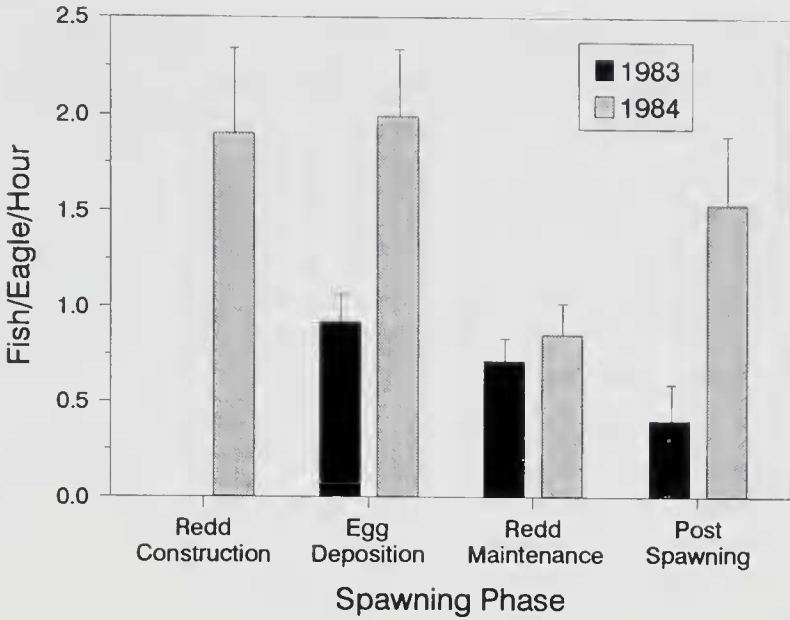


FIG. 7. Mean (+1 SE) fish take per hour by spawning phase, 1983 and 1984. Salmon spawning phases were: redd construction (RC), egg deposition (ED), redd maintenance (RM), and post spawning (PS).

hunting, as described by Hansen (1986), was scavenging by our definition. Given this distinction, we agree with Hansen (1986) that piracy requires more skill than scavenging. Further, Hansen (1986) and Knight and Skagen (1988) showed that size was a more important influence on the outcome of agonistic encounters than was age. Similar to hunting, however, the large size of salmon in their respective studies precluded the use of aerial foraging tactics, thus, agonistic foraging encounters were limited to ground piracy. Our observations at LMC were consistent with the view that younger birds are more likely to initiate ground piracy. However, factors other than size (e.g., maneuverability) may be more important for aerial piracy.

The lack of accumulation of carcasses during 1983 and corresponding lack of ground tactics did not allow us to assess differences in abilities of different age classes to acquire food by different methods in that year. Conditions during 1984 probably better reflected the ability of birds to obtain food under conditions when the potential for all tactics existed; during 1984, fish take using aerial tactics increased with age and using ground tactics decreased with age.

Verbeek (1977), Griffin (1981), and Fischer (1985) suggested that younger birds resort to pirating because of less skill at capturing food. We would extend their hypothesis to suggest that younger birds used ground tactics (i.e., scavenging and ground piracy) as a result of lesser skill at aerial tactics (i.e., aerial piracy or stooping). Several patterns that

we observed may, at first, appear inconsistent with this hypothesis. First, compared to other age classes, juveniles had higher fish take using aerial piracy and higher use of this tactic during 1983. We suggest this occurred because alternative foraging tactics were not available to juveniles in 1983. The lack of accumulated carcasses precluded the use of scavenging and ground piracy and we believe that juveniles lacked the ability to obtain sufficient food by stooping. Thus, aerial piracy was the only option for juveniles to obtain food at this time even though the overall fish take by this method was low. All other age classes obtained substantially more food by stooping.

Influence of prey availability on foraging behavior.—Bald Eagles shifted use of foraging methods at LMC as prey availability changed, both within and between years. Availability of salmon at LMC was influenced not only by abundance, but also by physical condition and location in the stream (e.g., deep pools or spawning sites).

During 1983, considerably fewer salmon and rapid consumption of available salmon precluded accumulations of carcasses. Consequently, the overall use of scavenging and ground piracy was considerably lower in 1983 than in 1984. Relatively few salmon carcasses were available for scavenging during the early spawning phases of 1984, but after egg deposition, salmon carcasses began accumulating rapidly, which resulted in a general trend of decreased use of stooping and increased use of scavenging and ground piracy.

During the post-spawning phase of 1984, when food had greatly diminished, older birds increased their use of aerial piracy, but they continued to forage primarily by stooping. There also was intense competition for the few dead or dying salmon that floated downstream; as weakened salmon died and floated to the surface, they were quickly taken by stooping eagles. During the post-spawning phase, each successful capture was accompanied by a flurry of aerial piracy attempts. Aerial piracy became the primary foraging method used by early subadults. We suspect this was a result of their inability to compete with adults or late subadults at stooping for the few remaining salmon. We did not quantify aerial chase parameters, but it was apparent that chases were longer in duration and more often resulted in physical contact during later spawning phases. Hansen et al. (1984) also found that the intensity of Bald Eagle aggression increased during periods of food shortage on the Chilkat River. Ground piracy and scavenging remained the primary foraging tactic for juveniles during this period, probably because they were unable to compete with older birds using stooping or aerial piracy.

Measures of foraging success.—Although we believe that our measure of fish take was reasonable for the comparisons we have made, it was a

biased estimate because we did not observe all foraging attempts; thus, our estimates of fish take should be regarded as a minimum. This could present problems if bias was not equal among comparison groups. Because adults were the most abundant age class and initiated the most foraging attempts, we would have expected to have missed more foraging attempts for this age class. The fact that our results showed fish take was highest for adults implies that our results were conservative, rather than in conflict. Similarly, time periods and years with the highest number of birds expected also occurred when fish take rates were highest. Thus, we believe that our conclusions were not exaggerated by observation bias; rather, we probably underestimated the differences among age classes or time periods.

Conservation implications.—Grier (1980) demonstrated that survival may be a relatively more important demographic influence than productivity in Bald Eagle populations. Thus, a lack of ability by younger birds to obtain food may be an important factor in survival (Stalmaster and Gessaman 1984). Our data are consistent with previous suggestions that the ability to obtain food increases with age for Bald Eagles (Stalmaster and Plettner 1992). Based on the formula presented by Stalmaster and Gessaman (1982:653), a Bald Eagle at LMC needed approximately 1.3 salmon/day in 1983 and 2.0 salmon/day in 1984 to meet minimum energy needs (differences due to disparity in mean salmon size between the two years). Adult eagles at LMC easily could have exceeded their minimum daily requirement during either year. In contrast, juveniles probably were at or below their minimum daily requirement, especially during 1983.

LMC provided older age classes of Bald Eagles with food that exceeded minimum energy requirements and we believe that younger birds benefitted as well, even though their food intake was lower than for older birds. Not only was food abundant and accessible in most years, but LMC also provided younger eagles an opportunity to observe adult foraging techniques. Because kokanee at LMC were relatively small, adult Bald Eagles used techniques requiring considerable skill not yet developed in young eagles. In both years there were approximately twice as many adults as all younger age classes combined. Before arrival at LMC, most juvenile eagles probably had little experience at foraging (McClelland et al. 1996).

If young eagles learn by observation and practice, the eagle concentration at LMC provided an exceptional opportunity for them to observe, emulate, and repeat foraging techniques used by adults. Thus, concentrations of food such as at LMC may be vital in enabling younger birds to acquire the necessary foraging skills, as well as being an important source of energy reserves for all age classes. Unfortunately, many salmon runs

throughout the Pacific Northwest, including the salmon run on which this study was based, have been devastated as a result of overfishing, habitat destruction, and mismanagement (Stalmaster 1987, Spencer et al. 1991).

ACKNOWLEDGMENTS

We are grateful to Teryl G. Grubb and an anonymous reviewer for their helpful suggestions on the manuscript. We appreciate David Patterson's advice and assistance with statistical analyses. We thank Elaine L. Caton, Victoria J. Dreitz, Patricia T. McClelland, and Richard Yates for their assistance. Mike Aderhold, John Fraley, and Jon Cavigli of the MDFWP allowed us to use unpublished data on salmon abundance. We appreciate the support provided by the National Park Service in GNP, and the logistical support provided by Rebecca Williams and other GNP interpretive personnel.

LITERATURE CITED

- AGRESTI, A. 1990. Categorical data analysis. John Wiley and Sons. New York, New York.
- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in Proc. second int. symp. inf. theory (B. Petrov and F. Czakil, eds.), Akademiai Kiado Budapest, Hungary.
- BENNETTS, R. E. AND B. R. MCCLELLAND. 1991. Differences in the distribution of adult and immature Bald Eagles at an autumn concentration in Montana. *Northwest Sci.* 65: 223–230.
- , ———, AND E. L. CATON. 1990. Aerial piracy by Bald Eagles: success of aggressors and followers. *Northwestern Nat.* 71:85–87.
- BROWN, B. T. 1993. Winter foraging ecology of Bald Eagles in Arizona. *Condor* 95:132–138.
- FISCHER, D. L. 1985. Piracy behavior of wintering Bald Eagles. *Condor* 87:246–251.
- FRALEY, J. 1984. Effects of the operation of Hungry Horse Dam on the kokance fishery in the Flathead River system. Annual Progress Report FY 1984. Montana Dept. Fish, Wildlife, and Parks, Kalispell, Montana.
- AND S. L. MCMULLIN. 1983. Effects of the operation of Kerr and Hungry Horse Dam on the kokanec fishery in the Flathead River system. Annual Progress Report FY 1983. Montana Dept. Fish, Wildlife, and Parks, Kalispell, Montana.
- GRIER, J. W. 1980. Modeling approaches to Bald Eagle population dynamics. *Wildl. Soc. Bull.* 8:316–322.
- GRIFFIN, C. R. 1981. Interactive behavior among Bald Eagles wintering in north-central Missouri. *Wilson Bull.* 93:259–264.
- HANSEN, A. J. 1986. Fighting behavior in Bald Eagles: a test of game theory. *Ecology* 67:787–797.
- , E. L. BOEKER, J. I. HODGES, AND D. R. CLINE. 1984. Bald Eagles of the Chilkat Valley, Alaska: ecology, behavior, and management. Final Rep. of the Chilkat River Bald Eagle Study. National Audubon Society, New York, New York.
- HARMATA, A. R. 1984. Bald Eagles of the San Luis Valley, Colorado: their winter ecology and spring migration. Ph.D. diss., Montana State Univ., Bozeman, Montana.
- HOSMER, D. W. AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York, New York.
- KNIGHT, R. L. AND S. K. SKAGEN. 1988. Agonistic asymmetries and the foraging ecology of Bald Eagles. *Ecology* 69:1188–1194.
- MCCLELLAND, B. R., L. S. YOUNG, D. S. SHEA, P. T. MCCLELLAND, H. L. ALLEN, AND E. B.

- SPETTIGUE. 1982. The Bald Eagle concentration in Glacier National Park, Montana: origin, growth, and variation in numbers. *Living Bird* 19:133–155.
- , P. T. MCCLELLAND, R. E. YATES, E. L. CATON, AND M. E. MCFADZEN. 1996. Fledging and migration of juvenile Bald Eagles from Glacier National Park, Montana. *J. Raptor Res.* 30:79–89.
- MCCOLLOUGH, M. A. 1989. Molting sequence and aging of Bald Eagles. *Wilson Bull.* 101:1–10.
- SAKAMOTO, Y., M. ISHIGURO, AND G. KITAGAWA. 1986. Akaike information criterion statistics. KTK Scientific Publications, Tokyo, Japan.
- SHIBATA, R. 1989. Statistical aspects of model selection. Pp. 215–240 *in* From data to model. (J. C. Williams, ed.). Springer-Verlag, New York, New York.
- SPENCER, C. N., B. R. MCCLELLAND, AND J. A. STANFORD. 1991. Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. *Bioscience* 41:14–21.
- STALMASTER, M. V. 1987. *The Bald Eagle*. Universe Books, New York, New York.
- AND J. A. GESSAMAN. 1982. Food consumption and energy requirements of captive Bald Eagles. *J. Wildl. Manage.* 46:646–654.
- AND ———. 1984. Ecological energetics and foraging behavior of overwintering Bald Eagles. *Ecol. Monogr.* 54:407–428.
- AND R. G. PLETTNER. 1992. Diets and foraging effectiveness of Bald Eagles during extreme winter weather in Nebraska. *J. Wildl. Manage.* 56:355–367.
- VERBEEK, N. A. M. 1977. Comparative feeding behavior of immature and adult Herring Gulls. *Wilson Bull.* 89:415–421.